INTERSPECIFIC HYBRIDIZATION IN LOBELIA L. SECTION LOBELIA[1]

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Abstract

The results of about 1400 pollinations that involved the 21 species of *Lobelia* L. sect. LOBELIA are reported. The bispecific combinations that gave positive or negative results are recorded. Thirty-three different species combinations are represented in the artificial interspecific hybrid populations. Two of these hybrids have been reported by previous authors.

Lobelia × ***rogersii*** hybr. nov. (*L. brevifolia* × *L. puberula*) is described. Numerous natural hybrid specimens were examined and the parentage was confirmed experimentally. Some plants of *L.* × *rogersii* were pollen-sterile; other plants were partly self-fertile.

Introduction

The phylogenetic relationships of 21 species of *Lobelia* L. sect. LOBELIA were discussed by Bowden (1959*a*). A detailed cytotaxonomic monograph of these species was presented in a series of papers (Bowden 1959*b*, 1960*a*, *b*). The results of about 1400 controlled pollinations are reported in the present series on interspecific hybridization in sect. LOBELIA.

There were two main purposes in the hybridization program: (1) to obtain interspecific hybrid plants and (2) to obtain evidence of hybridization barriers between certain of the 21 species. My first interspecific *Lobelia* hybrids were produced in 1940–41 at the Blandy Experimental Farm, Boyce, Virginia. The hybridization program was continued at Brantford, Ontario, from 1942 to 1947 and at the Department of Agriculture, Ottawa, from 1948 to 1958.

McVaugh (1943) and Wimmer (1953) listed natural and artificial hybrids of *L. siphilitica* × *L. cardinalis*. Artificial hybrids of this parentage have been produced over a period of several centuries by numerous hybridizers, for example Koelreuter (1777) and Gärtner (1849). Koelreuter (1777) also attempted to make crosses with other species of *Lobelia* but obtained negative results.

McVaugh (1936, 1943) and Wimmer (1953) listed the natural hybrid *L. brevifolia* × *L. puberula*. Wimmer (1953) proposed four hybrid parentages but Bowden (1959*a*) did not accept these formulae. Wimmer wrote "?*L. puberula* × *L. syphilitica* var. *ludoviciana*" as the possible parentage for *L. puberula* subsp. *pauciflora* (listed as *L. vaughiana*) but Bowden (1959*a*) rejected this formula. Wimmer (1953) listed "*L. georgiana* × *L. amoena*" and cited *Jewett 53*. Specimens of the latter were borrowed from the Goettingen Herbarium and proved to be the natural hybrid *L. brevifolia* × *L. puberula* (see below under *L.* × *rogersii*). Wimmer's "*L. amoena* × *L. puberula* = *L. azurea* Hort." was applied to a specimen from the Delessert Herbarium, which proved to belong to *L. amoena* Mx. Bowden (1959*a*) also rejected Wimmer's

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"*L. amoena* × *L. puberula*" as the parentage for *L. colorata* Sweet, which is a *nomen dubium*.

Materials and Methods

The materials of the parental species used in these crossing attempts have been listed by Bowden (1959*a*, *b*; 1960*a*, *b*). Three notebooks that list all of the accessions of the 21 species of *Lobelia* used during these investigations are deposited in the Library of the Plant Research Institute. Representative specimens of these species are deposited in the Phanerogamic Herbarium (DAO).

The cytological methods were described by Bowden (1959*b*). Pollen was examined in 1% potassium iodide and 1% iodine in 80% alcohol. Where the amount of normal pollen is stated as a percentage, the count was based on 100 pollen grains.

Controlled procedures were used for making the pollinations. Bowden (1959*a*) reported that plants of these 21 species of *Lobelia* were normally cross-pollinated but that many plants were self-fertile when tested. It was therefore necessary to emasculate the flowers early enough to prevent self-pollination. All artificially pollinated flowers were bagged before and after pollination to prevent contamination, particularly from pollen carried by insects. Some plants of a few species had sterile anther tubes (Bowden 1959*a*) and some of these plants provided good controls to test the crossing techniques.

In the racemes of the *Lobelia* species used during these hybridization attempts, the oldest flowers occurred toward the bases and the flowers were progressively less mature toward the apices. With experience, one could determine the following stages:

(*a*) Young flower with the anthers undergoing meiosis. At this stage, the short style was completely enclosed by the filament tube and the unopened stigma lobes were below the anther tube.

(*b*) Older stage, pollen immature and not yet powdery, style well-developed but the stigma lobes unopened and still below the anther tube. Flowers in stage (*a*) or (*b*) could be used for emasculation.

(*c*) Older flower with ripe powdery pollen which could be readily obtained for pollination by squeezing the anther tube gently so that the pollen (often yellow) poured out of the end.

(*d*) Mature flower with the style lengthened and pushed through the anther tube. When the end first emerged, the surfaces of the two stigma lobes were pressed together. This would be too early for pollination since the stigmatic surfaces would not be receptive and could not be reached for applying the pollen. As the flower matured, the stigma lobes separated and the two lobes could be easily observed. This was the stage when the pollen was applied in cross- or self-pollinations.

Cross-pollinations

For each interspecific crossing attempt, two to six flowers of the raceme of the seed parent were emasculated. Flowers were carefully selected so that they were neither too immature (early stage (*a*)) or too old (stage (*c*)). The desirable stage for emasculating the flowers was stage (*b*) in which the pollen was not

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yet powdery but in which the style was well-developed and the stigma lobes were still below the anther tube. The whole anther tube could be readily removed with forceps or it could be split longitudinally and removed in several pieces. In a flower with a large corolla, some of the corolla parts were removed to facilitate bagging. The other flowers of the raceme were removed and the emasculated raceme was then bagged, paper clips being used to keep the end of the bag tight against the raceme. Bamboo stakes were used to support delicate stems.

After emasculation and bagging, it was necessary to wait until the stigma lobes became receptive. This usually required several days to a week. Then pollen of the selected parent was applied to the stigmatic surfaces of the emasculated flowers. The anther tube of the pollen donor was held in forceps and placed next to the stigma lobes. Pressure on the anther tube caused the pollen to pour out of the end and the stigma lobes could be well dusted with pollen. The raceme was then rebagged.

Each attempted cross (or self) was labelled with an accession number which was recorded in a field notebook. Six field notebooks are deposited in the Library of the Plant Research Institute.

Self-pollinations

For self-pollinations, the anther tubes were left on the flowers. The lengthening of the styles through the anther tubes and the spreading of the stigma lobes were hastened by splitting the anther tubes longitudinally. This operation was done carefully so as not to damage the styles or stigma lobes. Each raceme was then bagged.

After a few days, the style had elongated and the stigma lobes had become receptive. Pollen from racemes of the same plant was applied to the stigma lobes of the flowers selected for self-pollination and the raceme was rebagged.

Effects of Pollination

Following cross- or self-pollination, several changes were noted within a few days if the pollen had acted as a stimulus or if fertilization had occurred. The corolla lobes withered quite promptly and the hypanthia began to swell. In some cases, the pollen acted as a stimulus and produced swollen but empty hypanthia.

Culture of the Hybrid Populations

Bowden (1959*a*) described the methods for growing populations of the 21 species of *Lobelia* sect. LOBELIA. The same methods were used for growing populations from the seed produced from the artificial cross- and self-pollinations. When the hypanthia were ripe, the material was placed in numbered envelopes which were stored at room temperature for several weeks to several months. The material was then sown in the greenhouse.

Since the seeds of *Lobelia* are small and since it was known that at least some of the species had light-sensitive seeds, the seeds of each hybrid accession were sown directly on the surface of moist seedling soil (John Innes mixture). Each pot was placed in a saucer of water and covered with a piece of window glass to prevent the seeds from splashing from one pot to another.

The seeds of the species of sect. LOBELIA germinated rather quickly, usually

within several weeks. The seeds from artificial cross-pollinations often germinated quickly and in large numbers, but sometimes germination was rather slow. When the seedlings had reached the small rosette stage, they were transplanted into small individual pots of John Innes potting soil, which was kept damp. The rosettes were repotted into larger pots when they grew large enough. Some plants flowered in the greenhouse but many of the plants were transplanted to field or garden plots in late May of each year. The hybrids grew well in the outside plots if the soil was kept thoroughly wet. Growth was satisfactory either in full sunlight or in partial shade.

Accession Numbers

Cross-pollinations were numbered numerically, X-1; X-2, etc. In each population, the seedlings were numbered consecutively; for example X-1-S1 means the first seedling of population X-1. In accessions resulting from self-pollinations, S was added after the main number and the individual seedlings were numbered consecutively; for example, X-357-S-S1 is the first seedling of accession X-357-S (a self-pollination).

General Results

About 1400 controlled pollinations were made. About 450 pollinations were self-pollinations or interstrain crosses within species, or self-pollinations of F_1 hybrids. About 547 pollinations were bispecific crosses (Table I). The remainder of the pollinations included backcrosses of F_1 hybrids to either parent, crosses between F_1 hybrids, and crosses between tetraploid hybrids and tetraploid species or tetraploid hybrids. Thirty-three different combinations of species (Table II) were represented in the populations of artificial interspecific hybrids. More than half of these hybrid combinations were bispecific but some tetraploid hybrids involved three, four, or five different species of sect. LOBELIA.

Self-pollinations of 16 of the 21 species showed that most plants were self-fertile but a few self-pollinations gave negative results. Interstrain crosses within each of *L. spicata*, *L. amoena*, *L. elongata*, *L. puberula*, *L. siphilitica*, and *L. cardinalis* usually gave positive results (much good seed) but a small percentage of the interstrain crosses in the last three species gave negative results.

In Table I, the positive results are the numbers of bispecific cross-pollinations that produced seeds that germinated and produced hybrid plants that flowered in the greenhouse or plots. A positive result usually indicates a cross that produced several to large numbers of hybrid plants. Occasionally only a single hybrid plant was obtained and either the rest of the seed did not germinate or the plants were albinos, green-white variegated, or very weak, and died when small.

In material from artificial pollinations that gave positive results, the seeds were usually well developed and plump, or reasonably so, and such seed germinated well. All material that seemed to have even slightly developed seeds was sown to make sure that any viable seed had an opportunity to germinate. Some of the abnormal seeds were undoubtedly not the result of fertilization, and this was proved in the case of the haploid plant of *L. puberula*

var. *puberula* reported by Bowden (1960*a*). This haploid was produced by female parthenogenesis that resulted from the stimulus of pollen of *L. georgiana*.

Populations grown from wild seed of species of sect. LOBELIA were relatively uniform in vigor. Some artificial hybrid populations showed much variation from strong plants that grew to maturity to small weak plants that survived for only a few weeks or months. Some populations of hybrids consisted only of weak plants. Some hybrid rosettes had green leaves; other hybrid seedlings were albino or had green-white variegated cotyledons and leaves. Some variegated plants produced green leaves as they matured. Most of the plants of the 33 hybrid combinations listed in Table II were strong or reasonably strong and some plants showed heterosis.

Certain combinations of species always gave negative results. For example, 20 crosses between *L. cardinalis* and *L. puberula* were made and 7 reciprocals; no viable seed was obtained (Table I). Other species combinations sometimes gave positive results and sometimes negative results. An example is the cross *L. siphilitica* × *L. cardinalis;* 56 attempts gave positive results and 16 attempts gave negative results (Table I).

The negative results include: (1) little or no swelling of the hypanthia and no seeds produced; (2) little or much swelling of the hypanthia, empty, or small brown ovules present, but no germination; (3) same as for (2) but some larger seed present that failed to germinate; occasionally seed was abundant and appeared to be normal but could not be germinated; (4) seed was sometimes obtained and germinated but the plants were albino, or green-white variegated, or weak, and died after several weeks or months.

As shown in Table I, many of the cross-pollination attempts gave negative results, usually either undeveloped hypanthia, or slightly or much enlarged hypanthia that were empty or had small brown ovules.

From Tables I and II, it is obvious that hybrid combinations could be made more easily at the tetraploid level than at the diploid level. It required 417 attempts to produce 119 positive results in diploid interspecific crosses. In tetraploid interspecific crosses, including crosses that involved tetraploid interspecific hybrids, 189 attempts produced 127 positive results.

Bowden (1959*a*, Fig. 1) published a chart that shows the phylogenetic relationships of the 21 species of *Lobelia* sect. LOBELIA. Some species are undoubtedly closely related and it is not surprising that they produced bispecific hybrids, for example *L. siphilitica* and *L. puberula*. Other species are very distinct morphologically but are closely related from the evolutionary viewpoint; they could be easily hybridized, for example *L. siphilitica* and *L. cardinalis*. A few F_1 hybrids were produced between more distantly related species. The unusual hybrids are: *L. puberula* × *L. feayana*, *L. flaccidifolia* × *L. feayana*, and *L. puberula* × *L. appendiculata*. In some crosses of closely related species, only negative results were obtained.

The positive production of an interspecific hybrid is easier to evaluate than a negative result. It is quite likely that additional positive hybrid combinations could be obtained if a large number of crosses were attempted, or if enough different variants of the parental species were used in making the crosses. Combinations of closely related species with the same chromosome number would be more likely to give positive results. In Table I, three attempts were

TABLE I

Results of bispecific cross-pollinations
(numerators: positive results; denominators: total number of attempts)

Seed parent	Pollen parent: *dorlmanna*	*kalmii*	*inflata*	*feayana*	*nuttallii, 2x*	*nuttallii, 4x*	*canbyi*	*boykinii*	*gattingeri*	*appendiculata*	*spicata*	*floridana*	*paludosa*	*flaccidifolia*	*glandulosa*	*amoena*	*elongata*	*georgiana*	*brevifolia*	*puberula*	*sphilitica*	*cardinalis*
dorlmanna, 2x																						
kalmii, 2x	0/1		0/1	0/1	0/1		0/1		0/1	0/1	0/2							0/1				
inflata, 2x		0/1		0/1	0/2		0/2		0/3	0/1	0/4									0/1	0/2	
feayana, 2x		0/1	0/1		0/2	0/1	0/1		0/1	0/2	0/2			0/1							0/1	
nuttallii, 2x				0/1			0/1															
nuttallii, 4x				0/1					0/1													
canbyi, 2x		0/1	0/1	0/1	1/1			0/2	1/2	0/2	0/1										0/1	
boykinii, 2x					0/1																	
gattingeri, 2x			0/1	1/1	0/1					0/1	0/3			0/1								
appendiculata, 2x			0/1		0/1		0/1		1/3		0/3			0/2					0/3			
: picata, 2x		0/1	0/2		0/1				0/4	0/2										0/1	0/1	

TABLE I (*Concluded*)

Seed parent	Pollen parent: *dortmanna*	*kalmii*	*inflata*	*feayana*	*nuttalii*, 2x	*nuttalii*, 4x	*canbyi*	*boykinii*	*gattingeri*	*appendiculata*	*spicata*	*floridana*	*paludosa*	*flaccidifolia*	*glandulosa*	*amoena*	*elongata*	*georgiana*	*brevifolia*	*puberula*	*siphilitica*	*cardinalis*
floridana, 6x													0/1	0/3	0/5	0/1	0/1	0/1	0/1	0/1		
paludosa, 6x												2/2		0/4	0/2			0/1	0/1			
flaccidifolia, 2x		0/1	0/1	1/1	0/2		0/1	0/2	0/3	0/4	0/3		0/1		0/1			0/3	0/2	1/3	0/3	0/1
glandulosa, 4x						0/1						0/1	0/1	0/5		2/5	1/1	0/5	0/5	0/1		
amoena, 4x						0/1	0/1						0/1	0/1	3/4		2/2	0/3	0/1	0/7	0/2	
elongata, 4x				0/1		0/1						0/1	0/3	0/4	2/4	3/5		0/4	0/2	0/8	0/7	
georgiana, 2x			0/1	0/1			0/1	0/1	0/1	0/1	0/2		0/1	0/8	1/2	0/3	0/1		1/4	1/11	2/3	0/2
brevifolia, 2x		0/1	0/1	0/1			0/2	0/1	0/2	0/1	0/1			0/6				1/2		4/6	0/6	0/2
puberula, 2x		0/1	0/4	1/1			0/1			3/3	0/6			0/7	0/1	0/3	0/1	2/7	3/7		0/7	0/7
siphilitica, 2x		0/1	0/3						0/2		0/1			0/4	0/2	0/3	0/2	3/4	1/3	19/27		56/72
cardinalis, 2x			0/1												0/1			0/3	0/1	0/20	15/27		

TABLE II

Artificial interspecific *Lobelia* hybrids
(seed parent first, pollen parent second)

Bispecific diploid hybrids

1. *L.* × *rogersii* (*L. brevifolia* × *L. puberula;* and reciprocal); *L. brevifolia* × *L.* × *rogersii.*
2. *L.* × *speciosa* (*L. siphilitica* × *L. cardinalis;* and reciprocal; see No. 16);
   L. × *speciosa* × *L. cardinalis;* and reciprocal;
   L. × *speciosa* × *L. siphilitica;* and reciprocal.
3. *L. puberula* × *L. georgiana;* and reciprocal;
   (*L. puberula* × *L. georgiana*) × *L. puberula;* and reciprocal;
   (*L. puberula* × *L. georgiana*) × *L. georgiana;* and reciprocal.
4. *L. siphilitica* × *L. puberula;* see No. 17.
5. *L. siphilitica* × *L. georgiana;* and reciprocal.
6. *L. siphilitica* × *L. brevifolia.*
7. *L. georgiana* × *L. brevifolia;* and reciprocal.
8. *L. puberula* × *L. feayana.*
9. *L. flaccidifolia* × *L. puberula.*
10. *L. flaccidifolia* × *L. feayana.*
11. *L. puberula* × *L. appendiculata.*
12. *L. canbyi* × diploid *L. nuttallii.*
13. *L. canbyi* × *L. gattingeri.*
14. *L. gattingeri* × *L. feayana.*
15. *L. appendiculata* × *L. gattingeri.*

Bispecific tetraploid hybrids and one triploid hybrid

16. Tetraploid *L.* × *speciosa* (*L. siphilitica* × *L. cardinalis*); see No. 2;
    tetraploid *L.* × *speciosa* × tetraploid *L. siphilitica;*
    tetraploid *L.* × *speciosa* × tetraploid *L. cardinalis;*
    tetraploid (*L. cardinalis* × *L.* × *speciosa*);
    triploid *L.* × *speciosa* (backcross involving *L. cardinalis*).
17. Tetraploid (*L. siphilitica* × *L. puberula*); see No. 4.
18. *L. glandulosa* × *L. elongata;* and reciprocal;
    L. elongata × (*L. glandulosa* × *L. elongata*).
19. *L. georgiana* (unreduced gamete) × *L. glandulosa.*
20. *L. elongata* × tetraploid *L. cardinalis.*
21. *L. amoena* × *L. elongata;* and reciprocal.
22. *L. amoena* × *L. glandulosa;* and reciprocal.

Complex tetraploid hybrids

23. (*L. elongata* × *L. glandulosa*) × *L. amoena.*
24. Tetraploid (*L. siphilitica* × *L. puberula*) × *L. elongata.*
25. Tetraploid (*L. siphilitica* × *L. puberula*) × *L. glandulosa.*
26. Tetraploid (*L. siphilitica* × *L. puberula*) × tetraploid *L. cardinalis.*
27. Tetraploid (*L. siphilitica* × *L. puberula*) × tetraploid *L.* × *speciosa;* and reciprocal.
28. Tetraploid (*L. siphilitica* × *L. puberula*) × ((*L. elongata* × tetraploid *L.* × *speciosa*) × *L. elongata*).
29. *L. amoena* × tetraploid *L.* × *speciosa;* and reciprocal.
30. *L. glandulosa* × tetraploid *L.* × *speciosa;* and reciprocal.
31. *L. elongata* × tetraploid *L.* × *speciosa;* and reciprocal;
    (*L. elongata* × tetraploid *L.* × *speciosa*) × *L. elongata.*
32. (*L. elongata* × tetraploid *L.* × *speciosa*) × *L. amoena.*
33. (*L. elongata* × tetraploid *L.* × *speciosa*) × *L. glandulosa;*
    tetraploid *L.* × *speciosa* × (*L. elongata* × *L. glandulosa*).
34. (tetraploid *L.* × *speciosa* × (*L. elongata* × *L. glandulosa*)) × (*L. elongata* × *L. amoena*).

Bispecific hexaploid hybrid

35. *L. paludosa* × *L. floridana.*

made to cross *L. siphilitica* with *L. brevifolia* and six attempts were made to produce the reciprocal cross. Only one attempt produced viable seed. The fact that there are so few natural interspecific hybrids in sect. LOBELIA, except for *L.* × *rogersii* (*L. brevifolia* × *L. puberula*), indicates that there are strong barriers to hybridization between these species as they grow under natural conditions.

The F_1 hybrids usually had the same chromosome number as the parental species. There were four exceptions: (1) In *L.* × *speciosa* (*L. siphilitica* × *L. cardinalis*), most F_1 hybrids were diploid as were the parental species. Several populations showed a mixture of self-sterile diploids ($2n = 14$) and spontaneous self-fertile tetraploids ($2n = 28$). Populations of tetraploid *L.* × *speciosa* were also developed by colchicine treatments. (2) Three triploids were produced from the cross tetraploid (*L. cardinalis* subsp. *graminea* cv. 'Queen Victoria' × *L.* × *speciosa*) × diploid *L. cardinalis* subsp. *graminea* cv. 'Illumination'. (3) In *L. siphilitica* × *L. puberula*, most F_1 hybrids were diploid like the parental species, but in one population there was a mixture of diploids and self-fertile tetraploids. The tetraploids were either the result of zygotes formed from unreduced gametes or by the spontaneous doubling of the chromosome number of the zygotes, or the result of the doubling of the chromosome number of the zygotes caused by accidental spraying of the seedlings with NNOR spray. (4) In the cross *L. georgiana*, $2n = 14$, × *L. glandulosa*, $2n = 28$, the single F_1 hybrid was tetraploid so there must have been an unreduced gamete from *L. georgiana*.

Cytotaxonomy of Interspecific *Lobelia* Hybrids

It is planned to present the cytotaxonomic data for the 33 hybrids listed in Table II in four papers. *Lobelia* × *rogersii* hybr. nov. is described in the last part of the present paper.

Natural interspecific hybrids that involve species of *Lobelia* sect. LOBELIA occur only rarely. At present, only two natural hybrids are known, namely *L.* × *speciosa* Sweet (*L. cardinalis* L. × *L. siphilitica* L.) and *L.* × *rogersii* hybr. nov. (*L. brevifolia* Nutt. × *L. puberula* Mx.). Artificial hybrids were produced during the present investigations that confirm the putative parentages of these two hybrids.

Since a large amount of data has accumulated on *L.* × *speciosa*, it will be treated in a later paper. Only four records of natural hybrids of *L.* × *speciosa* are known but this hybrid has been produced artificially by numerous hybridizers for several centuries. During these investigations, many different diploid and tetraploid nothomorphs and a few triploid nothomorphs of *L.* × *speciosa* have been grown. Natural hybrid specimens of *L.* × *rogersii* occur relatively frequently because some plants are partly fertile.

For each different combination of parental species, the following data are recorded: (1) parentage; (2) morphology of the hybrids; (3) somatic chromosome number ($2n$), and meiotic chromosome behavior, usually MI or diakinesis, and chromosome number (n); (4) pollen characteristics; (5) sterility or fertility of the hybrids when tested by self-pollination; and (6) voucher specimens.

In the formulae of parentages of artificial hybrids, the seed parent (♀) is always given first (before the ×) and the pollen parent (♂) is given second.

In the case of natural hybrids, the order of the specific names is alphabetical.

Herbarium specimens were made of representative artificial hybrid plants and voucher specimens are cited under each hybrid combination. The main set of specimens of the artificial hybrids is deposited in the Phanerogamic Herbarium of the Plant Research Institute (DAO). Some duplicate specimens of some hybrid populations have also been deposited at various herbaria (NY, MICH, MO, US, GH, BH, K, and W) and a smaller number of duplicates at several other herbaria. Specimens of natural hybrids were examined from several herbaria: DAO, NY, CM, LSU, and GOET. The symbols for herbaria are those of Lanjouw and Stafleu (1959).

Lobelia × *rogersii* hybr. nov., a Bispecific Diploid Hybrid

1. *Lobelia* × ***rogersii*** Bowden, hybr. nov.

Parentage.—*L. brevifolia* Nutt. × *L. puberula* Mx.

Syn.—*L. glandulosa sensu* A.DC. *in* DC. Prodr. Syst. Veg. **7**, 378 (1839); in part, *nec* Walter, 1788.

L. amoena var. *glandulifera* A. Gray, *pro parte, typo excluso*, Syn. Fl. **2**, 4 (1878).

L. brevifolia × *L. puberula*, *in* McVaugh, Rhodora, **38**, 291–292 (1936); and *in* McVaugh, North American Fl. **32A**(1), 76 (1943).

L. brevifolia × *L. puberula*, *in* Wimmer, Pflanz. Reg. veg. consp. IV. 276b (Heft 107), p. 430 (1953).

L. georgiana × *L. amoena*, *in* Wimmer (1953, p. 429).

Hybrida inter brevifoliam et puberulam stans; caulis erectus, breviter pubescens, (20)–30–40–(115) cm alt.; folia (18)–20–27 in caule, minora 1–2 cm, media (3)–4–6–(8) cm long., in margine remote et inaequaliter denticulata vel infrequenter subintegra; folia ab oblongis vel ellipticis late oblanceolata vel lanceolata; bractae florum conspicuae, margine variabiles, similes marginum foliorum sed nonnunquam acute serratae; pedicelli puberuli; flores 14–24 mm long.; tubus ex filamentis 5–6–(9) mm long.; auriculae calycis conspicuae; lobi calycis plerumque acutissime serrati; hypanthium plerumque hirsutum vel infrequenter glabrum; tubus antherarum 2–3–(4) mm long.; antherae steriles et pallidae vel aliquantulum fertiles et griseae sive nigrescentes.

Stems erect, short-pubescent, (20)–30–40–(115) cm high; (18)–20–27 cauline leaves, small-sized, 1–2 cm, to medium-sized, (3)–4–6–(8) cm long, margins remotely and irregularly denticulate or rarely subentire; leaves oblong or elliptic to broadly oblanceolate or lanceolate; flower bracts conspicuous, the margins variable, similar to the leaf margins and sometimes sharply serrate; pedicels puberulent; flowers 14–24 mm long including the hypanthium; filament tube 5–6–(9) mm long; calyx auricles conspicuous; calyx lobes usually very sharply serrate; hypanthium usually hirsute, rarely glabrous; anther tube 2–3–(4) mm long, pale-colored and pollen-sterile or gray or dark-colored, the colored anther tubes with some pollen.

Lobelia × *rogersii* is named in honor of Dr. Rogers McVaugh, who has made valuable contributions to knowledge of the taxonomy and distribution of the North American species of *Lobelia*.

The typical nothomorph of *L.* × *rogersii* is represented by the holotype and

hortotype collection, X-949, and by two paratype collections, X-945 and X-1282. These specimens are artificial hybrids of the parentage *L. brevifolia* Nutt. × *L. puberula* Mx. f. *puberula*, or reciprocal, and are listed under 1*a*. Under 1*b*, 1*c*, and 1*d*, there are listed other nothomorphs of *L.* × *rogersii*, and these have slightly different parentages which, respectively, involve *L. puberula* f. *simulans*, var. *mineolana*, and subsp. *pauciflora*. Specimens of natural hybrids are listed under 1*e*. Except for the single specimen of 1*d* in which the parentage involved subsp. *pauciflora*, the specimens closely resemble one another. It therefore seems unwise to name each of the different nothomorphs. If any of the nothomorphs are validly named in the future, the typical nothomorph will automatically be called nm. *rogersii*. The specimens cited under 1*b*, 1*c*, 1*d*, and 1*e* are paratypes of *L.* × *rogersii* but are not paratypes of the typical nothomorph.

Specimens of *L.* × *rogersii* can be readily distinguished from either parent. Plants of *L. brevifolia* have smaller and more numerous cauline leaves while specimens of *L. puberula* have larger cauline leaves and usually the calyx lobes have entire margins. Specimens of *L.* × *rogersii* might be confused with *L. georgiana* but can be distinguished by the broad bases of the calyx lobes, the conspicuous auricles, and the smaller leaves. Plants of *L. flaccidifolia* differ from *L.* × *rogersii* in the longer, narrower cauline leaves with thin leaf blades.

1*a*. *Lobelia* × *rogersii* Bowden, typical nothomorph

Parentage.—*L. brevifolia* Nutt. × *L. puberula* Mx. subsp. *puberula* var. *puberula* f. *puberula;* and reciprocal.

Morphology

The hypanthia of all specimens of X-949 and X-945 have coarse white hairs but the pubescence is less dense in some specimens. In X-1282, one specimen, S1, has dense white hairs on the hypanthia while two specimens have almost glabrous hypanthia. All but one specimen (X-949-S10) have prominent teeth on the calyx lobes.

Chromosome Behavior

Diakinesis in X-949-S6, the holotype of *L.* × *rogersii*, was studied and there were 7 II + 2 sup. per cell in 15 PMC's. In a hortotype, X-949-S2, MII and Telophase II showed $n = 7 + 1$ sup. Both parents of X-949 had $2n = 14 + 1$ sup. At diakinesis in a paratype, X-945-S8, there were 7 II + 2 sup. per cell in 18 PMC's and 6 II + 2 I + 2 sup. per cell in 2 PMC's.

Pollen

The anther tubes of the type collection, X-949, were pale-colored. In X-949-S1, the anthers had a little abnormal pollen. In X-1282-S3, the anther tubes were dark-colored; the pollen was abundant and there were 86 normal grains and 14 abnormal pollen grains. The abnormal pollen grains were much smaller and some grains were irregularly shaped. The pollen of two specimens of *L. puberula* and *L. brevifolia* was respectively 95% and 97% normal.

Sterility–Fertility

A plant of X-945-S2 was self-pollinated. One medium-sized hypanthium was harvested and it had a fair number of good seeds and some shrivelled seeds.

Five F_2 plants were grown. A plant of *L. brevifolia*, 7-1-B-S2, was pollinated with pollen of the F_1 hybrid, X-945-S1, and two medium-sized hypanthia were obtained. Eight backcross hybrids were grown.

Voucher Specimens

X-949: *L. brevifolia*, 7-1-B-S2, St. Tammany Parish, Louisiana, × *L. puberula* f. *puberula*, 6-13-B-S15, Dare County, North Carolina. X-949-S6, greenhouse, January 4, 1954, holotype of *L.* × *rogersii*, typical nothomorph. The following seven greenhouse specimens from the same population are hortotypes of the typical nothomorph and were prepared from September 1, 1953, to March 8, 1954: X-949-S1, S2, S11, S5, S10, S8, and S7.

X-945: *L. brevifolia*, 7-1-B-S1, St. Tammany Parish, Louisiana, × *L. puberula* f. *puberula*, 6-14-B-S5, Tyrell County, North Carolina. X-945-S1, greenhouse, September 29, 1953, and X-945-S8, greenhouse, January 4, 1954. Both are paratypes of the typical nothomorph.

X-1282: *L. puberula* f. *puberula*, 107-54-S6, 6 miles east of Williamston, North Carolina, × *L. brevifolia*, 7-2-S6, Mobile Co., Alabama. X-1282-S1 and S2, greenhouse, August 14, 1956. X-1282-S3, greenhouse, August 20, 1956. All three are paratypes of the typical nothomorph.

1*b*. *Lobelia* × *rogersii* Bowden, second nothomorph

Parentage.—L. *puberula* Mx. subsp. *puberula* var. *puberula* f. *simulans* (Fern.) Bowden × *L. brevifolia* Nutt.; and reciprocal.

Morphology

Three specimens have calyx lobes with prominent teeth while two specimens (X-1241-S3 and -S5) have fewer teeth on the calyx lobes. All of the specimens of X-1241 have pubescent hypanthia while the specimen of X-1274 has glabrous hypanthia.

Pollen

In X-1241-S3, the anther tubes were dark-colored. The pollen was abundant and 92% of the grains were normal. Four specimens of X-1241 and X-1274 had dark-colored anther tubes while one specimen, X-1241-S5, had pale-colored anther tubes.

Sterility–Fertility

An F_1 hybrid, X-1241-S2, was self-pollinated. Two small hypanthia were harvested and these contained a fair amount of seed which germinated. Three F_2 plants were grown.

Voucher Specimens

X-1241: *L. puberula* f. *simulans*, 6-6-B-S4, Buncombe Co., North Carolina, × *L. brevifolia*, 7-4-S5, Hancock Co., Mississippi. X-1241-S1 and S5, greenhouse, August 8, 1956. X-1241-S3, greenhouse, July 25, 1956. X-1241-S4, greenhouse, July 27, 1956.

X-1274: *L. brevifolia*, 7-2-S5, Mobile County, Alabama, × *L. puberula* f. *simulans*, 6-6-B-S4, Buncombe Co., North Carolina. X-1241-S1, greenhouse, August 28, 1956.

1*c*. *Lobelia* × *rogersii* Bowden, third nothomorph

Parentage.—L. *puberula* Mx. subsp. *puberula* var. *mincolana* Wimmer × L. *brevifolia* Nutt.

Morphology

There are scattered short hairs on the hypanthia of the three specimens of X-1401 and the flower bracts are consistently large. Specimens of the typical and second nothomorphs usually have smaller flower bracts, but, in X-1282 and X-1241, the flower bracts are quite large.

Pollen

In X-1401, the anther tubes were dark-colored and the pollen was abundant. In X-1401-S1, there were 40 normal to 60 abnormal pollen grains.

Voucher Specimens

X-1401: *L. puberula* var. *mincolana*, 6-20-S1, Union Parish, Louisiana, × *L. brevifolia*, 7-4-S5, Hancock Co., Mississippi. X-1401-S3 and S4, greenhouse, May 13, 1957. X-1401-S1, greenhouse, May 21, 1957.

1*d*. *Lobelia* × *rogersii* Bowden, fourth nothomorph

Parentage.—*L. brevifolia* Nutt. × *L. puberula* Mx. subsp. *pauciflora* (Bush) Bowden.

Morphology

Two hypanthia of X-947 (original cross to produce seed for F_1) were harvested. Good seed was collected but only a few germinated. Most of the seedlings had white cotyledons and died. One seedling produced green leaves but the mature plant (S2) was weak and only 25 cm high. The raceme is few-flowered. The hypanthia are densely hirsute and the calyx lobes are few-toothed and have the shape of the calyx lobes of subsp. *pauciflora*.

Pollen

The anther tubes were quite pale-colored and shrivelled.

Voucher Specimen

X-947: *L. brevifolia*, 7-1-B-S1, St. Tammany Parish, Louisiana, × *L. puberula* subsp. *pauciflora*, 6-11-S3, Freestone Co., Texas. X-947-S2, greenhouse, February 2, 1954.

1*e*. *Lobelia* × *rogersii* Bowden, natural hybrid specimens, undetermined nothomorphs

Parentage: L. brevifolia Nutt. × *L. puberula* Mx. subsp. *puberula*.

Numerous natural hybrid specimens of *L.* × *rogersii* have been collected in the area where *L. brevifolia* and *L. puberula* grow together or in adjacent habitats, namely in west Florida, Alabama, Mississippi, and eastern Louisiana. *Lobelia puberula* subsp. *pauciflora* can be eliminated as a possible parent of these natural hybrids since it occurs in a small area in eastern Texas and western Louisiana which is west of the geographical range of *L. brevifolia*. The *L. puberula* subsp. *puberula* parent of these natural hybrids could have been var. *puberula* f. *puberula* or f. *simulans*, var. *mincolana*, or var. *obtusifolia* (A.DC.) Fern.

Since some of the artificial F_1 hybrids of *L.* × *rogersii* were partly fertile, some of the natural hybrid specimens might be F_1 or F_2 plants or later generations, backcrosses to either parent, crosses between different generations or between different generations and backcrosses. The natural hybrids closely resemble the specimens of *L.* × *rogersii* that are cited under 1*a* and 1*b*.

Pollen

In *Brown 5444* from Louisiana, the anthers were dark-colored. The pollen was abundant and 94% normal. In Demaree *36258-A* from Mississippi, the anther tubes were pale-colored and shrivelled in one specimen; the other specimen had dark-colored anther tubes and the pollen was abundant and 85% normal. In *Harvill et al.* from Alabama, the anther tubes of two racemes were pale-colored and shrivelled; the anther tubes of a third raceme were dark-colored and the pollen was 45% normal.

Specimens Examined

FLORIDA: West Florida, *Chapman s.n.* (NY). ALABAMA: *Gates s.n.* (GH; NY). The GH specimen is mounted on the same sheet as the type of *L. georgiana* McVaugh. The NY specimen was identified as *L. glandulosa* by De Candolle. Lee Co.: Auburn, *Earle s.n., September 28, 1896*, two sheets (CM); *Earle s.n., October 4, 1896* (NY); *Earle s.n., October 15, 1896* (CM). Washington Co.: Growing on damp sandy soil near the highway about 5 miles south of Tibbie, *Harvill, Crawford & Segars s.n., October 23, 1949* (DAO). Mobile Co.: Mobile, *Jewett 53*, two sheets (GOET). MISSISSIPPI: Kashtaw, *Tracy 4940* (NY). Harrison Co.: Biloxi, *Tracy s.n., October 27, 1899* (NY). Jackson Co.: Ocean Springs, *Earle s.n., October 27, 1889* (CM). Perry Co.: Ridge thickets, game reserve, Maxie, De Soto National Forest, *Demaree 36258-A* (DAO). LOUISIANA: Washington Parish: Moist bottoms, in longleaf pine hills, L.S.U. Forestry Camp, 10 miles west of Bogalusa, *Brown 5444* (LSU; photograph and fragment, DAO).

Lobelia × *rogersii* occurs naturally where populations of *L. brevifolia* and *L. puberula* occur in the same or adjacent habitats. Some of the natural and artificial hybrid plants are pollen-sterile while some of the artificial hybrids that were tested were partly self-fertile. *Lobelia* × *rogersii* has been collected rather frequently, undoubtedly because F_1 hybrids are produced quite often, but also because later generations and backcrosses, etc., also probably occur frequently. *Lobelia* × *rogersii* is therefore behaving partly as a newly formed hybrid and partly as a recently produced species of hybrid origin. The two parental species, *L. brevifolia* and *L. puberula*, are so different morphologically from one another that I consider them to be distinct species. *Lobelia brevifolia* is closely related to *L. puberula* and has probably been derived from it. *Lobelia puberula* has a relatively large range in the eastern United States while *L. brevifolia* is restricted to a small range along the Gulf Coast.

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References

BOWDEN, W. M. 1959*a*. Phylogenetic relationships of twenty-one species of *Lobelia* L. section LOBELIA. Bull. Torrey Botan. Club, **86**, 94–108.

——— 1959*b*. Cytotaxonomy of *Lobelia* L. section LOBELIA. I. Three diverse species and seven small-flowered species. Can. J. Genet. Cytol. **1**, 49–64.

——— 1960*a*. Cytotaxonomy of *Lobelia* L. section LOBELIA. II. Four narrow-leaved species and five medium-flowered species. Can. J. Genet. Cytol. **2**, 11–27.

——— 1960*b*. Cytotaxonomy of *Lobelia* L. section LOBELIA. III. *L. siphilitica* L. and *L. cardinalis* L. Can. J. Genet. Cytol. **2**, 234–251.

GÄRTNER, C. F. V. 1849. Versuche und Beobachtungen über die Bastarderzeugung im Pflanzenreich. Stuttgart.

KOELREUTER, I. T. 1777. Lobeliae hybridae. Acta Acad. Sci. Imp. Petropol. **1**(2), 185–192 and tab. IV. (Apparently published in 1780.)

LANJOUW, J. and STAFLEU, F. A. 1959. Index Herbariorum. Part I. The herbaria of the world. 4th ed. Regnum Vegetabile, **15**. Utrecht.

MCVAUGH, R. 1936. Studies in the taxonomy and distribution of the eastern North American species of *Lobelia*. Rhodora, **38**, 241–263; 276–298; 305–329; and 346–362.

——— 1943. Campanulaceae (Lobelioideae). North American Flora, **32A**(1), 1–134. The New York Botanical Garden, New York.

WIMMER, F. E. 1953. Campanulaceae–Lobelioideae. Teil II. Tribus II. Lobeliae Presl. Das Pflanzenreich Regni veg. consp. IV. 276b (Heft 107). Akad.-verlag, Berlin. pp. 261–813.